COMPARISON OF THE SELFED PROGENY AND TESTCROSS PROGENY METHODS OF MAIZE IMPROVEMENT

By

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With the advent of single cross corn hybrids, breeders have become interested in increasing the yield of parental lines per se and the hybrids developed using these inbred lines. The purpose of this study was to obtain additional information on the effectiveness of the S_2 progeny and inbred tester methods. The materials used were derived from an on-going project in maize breeding at the University of Florida initiated in 1975. Three cycles of selection in two unrelated populations, A and B, had been completed in 1984.

To compare the two methods, four experiments were conducted: (1) one hundred F_1 hybrids among 20 selected cycle 3 lines (five from each population and method) were tested at two locations; (2) bulked populations of the Syn-1, S_1, and S_2 generations from intercrosses among selected cycle 3 lines from each population and method were tested at two locations for two years; (3) bulks of selected cycle 4 lines from each population and method were tested at two locations; and (4) cycle 4 S_2 lines and their testcrosses were evaluated at one location for one year. Data on yield and other traits were collected and analyzed.

The testcross method gave significantly better progress than the S_2 progeny method for combining ability in all traits. Nevertheless, a few lines from the S_2 progeny method had combining ability (GCA) as good as the best lines from the inbred tester method. The S_2 progeny method resulted in significantly less inbreeding depression than the testcross method for grain yield of cycle 3 populations, producing more vigorous lines in the S_1 and S_2 generations. There was a significant positive correlation between S_2 lines and their testcrosses, which indicates that visual selection among lines in one environment may be effective for the elimination of undesirable traits in hybrids, especially for stalk strength, ear height and husk score. These results suggest that the two methods emphasized different types of gene action and that overdominant gene action may exist at some loci. More cycles of selection are needed to determine the long-term effects of these contrasting breeding methods.

Chairman

INTRODUCTION

Various methods of recurrent selection have been used for maize (Zea mays L.) improvement. Breeders have continued to search for more reliable breeding value measurements of individual plants or lines chosen as parents for the next cycle. Maize breeding has evolved through several stages during the past 100 years.

The first breeding method used in corn was mass selection. This type of selection generally implied phenotypic selection on an individual basis for the improvement of a population for some specific trait. Varietal hybridization suggested by Beal (1880) was the next breeding method. The ear-to-row system of breeding was devised by Hopkins (1899). This method involved selecting a group of ears, planting these ear-to-row and obtaining information on progeny performance. The next method, suggested by Shull (1910), involved selection within and among inbred lines and the evaluation of the lines in F_1 hybrid combinations. Jones (1918) proposed the double-cross method that made hybrid corn economically feasible.

Preliminary screening techniques by Davis (1927) and Jenkins and Brunson (1932) showed that the topcross test was effective for discarding lines that did not have satisfactory performance in hybrids. Early (S_1 or S_2 generation) testing of inbred lines was proposed by Jenkins (1935) and Sprague (1939). With this procedure, phenotypically desirable S_0 plants are crossed with one or more common testers and the combining abilities of the S_0 plants are estimated on the basis of test-cross performance. Lonnquist (1949) proposed that the amount of testing could be reduced by crossing S_1 progenies with the tester, and discarding on the basis of progeny row observation before making tests for combining ability of the newly derived inbred lines.

Reports from Genter and Alexander (1962) and Burton et al. (1971) indicated that dominant genes of the tester may mask genetic differences between lines. S_1 line per se selection has been suggested to solve this difficulty. However, increases in the frequencies of favorable alleles at those loci affecting grain yield should be greater with S_2 selection than with S_1 line selection since at $p = 0.5$ additive variance among S_2 lines is 1.5 times as large as among S_1 lines (Horner et al. 1969).

A number of short-term experiments have compared selfed S_1 progeny testing with testcross progeny testing. Both methods have been efficient, with no clear difference between methods after various cycles of selection.

In a search for more accurate methods of genotype evaluation, a project in maize breeding at the University of Florida was designed in 1975 with the purpose of comparing two quite different selection methods. One method is based on performance of S_2 lines per se since selfed progeny evaluation avoids the masking effect of testers (resulting in higher heritability estimates). The second method is based on the performance of testcrosses involving S_2 lines crossed with an inbred tester. For the latter, an inbred line from Population A was used as a tester to evaluate S_2 lines from Population B, and likewise a line from B was used as a tester to evaluate S_2 lines from A.

The objectives of this study were 1) to determine the effects of the S_2 progeny and testcross selection methods on vigor of inbred lines derived from third and fourth cycle populations and on inbreeding depression, 2) to determine the effects of these breeding methods on general combining ability (GCA) and specific combining ability (SCA) of derived populations and lines, and 3) to correlate S_2 parents with testcross performance.

LITERATURE REVIEW

Gene Action

The development of more efficient breeding procedures requires an understanding of the types of gene action governing the inheritance of quantitative traits (Comstock and Robinson, 1952; East, 1936; Eberhart et al., 1966; Gardner et al., 1953; Gardner and Lonnquist, 1959; Gardner, 1963; Jones, 1917; Lindsey et al., 1962; Moll and Robinson, 1967; Sprague et al., 1959; Robinson et al., 1955; and Russell, 1971). The theoretical considerations of the role of overdominance and the accumulation of favorable dominant genes at numerous loci as possible explanations of heterosis have been a source of controversy for years among geneticists, as well as plant and animal breeders (Penny et al., 1962).

Jones (1917) and East (1936) were the first to suggest the type of gene action in corn. The former suggested the dominant favorable linked-gene hypothesis. The latter proposed a heritable mechanism in maize involving multiple alleles in which certain of the heterozygous genotypes possible at a given locus are superior to any of the possible homozygous genotypes. Jenkins (1940) suggested that yield in corn was controlled by a large number of dominant genes having approximately equal effects. Crow (1948) and

Brieger (1950) indicated that the dominance hypothesis by itself is inadequate to explain all of the facts of heterosis.

The first attempt to estimate different types of gene action involved in single cross yield heterosis was provided by Sprague and Tatum (1942). Their separation recognized two categories: general and specific combining ability. Differences in general combining ability (GCA) involve additive effects, while specific combining ability is due to non-additive effects. To utilize additive effects, they suggested recurrent selection for GCA. On the other hand, Hull (1945) concluded that yield heterosis was conditioned by overdominance as well as partial and complete dominance. For this type of gene action, recurrent selection for specific combining ability (SCA) was proposed. Hull's breeding plan involved the use of homozygous lines as testers. Comstock et al. (1949) proposed reciprocal recurrent selection (RRS) as a method to utilize both GCA and SCA together. Genetic divergence per se between the two source populations is not a requirement for the success of RRS, as shown by Griffing (1962) and Cress (1966). S_0 or S_1 plants from source A are selfed-pollinated and outcrossed to several plants from source B. Seeds obtained on the latter are bulked, and the resulting testcrosses are evaluated in different environments. The parents of selected testcrosses are interbred, using the selfed seed produced the first year, to obtain a new population. Source B plants are evaluated against several source A tester plants in the same way. The steps are repeated in subsequent cycles. Comstock et al. (1949) pointed out that the method was definitely superior to selection for GCA for loci at which there is overdominance, and to the SCA method suggested by Hull for loci at which there is partial dominance. In view of the possibility of overdominance at some loci and the probability of partial dominance at other loci, there is good reason to believe that RRS would be more efficient than either selection for GCA or SCA alone.

Horner et al. (1973) evaluated five cycles of recurrent selection using an inbred line and the parental population as testers and S_2 progeny performance per se. They reported a 4.4% yield gain per cycle from the inbred tester method compared with 2.4 and 2.0% for the parental tester and S_2 progeny methods, respectively. They indicated that the inbred tester method was evidently more effective for improving breeding populations and developing elite single crosses. Zambezi et al. (1986) reported further evidence that inbred testers can be used successfully for improving GCA as well as SCA in corn.

The effectiveness of RRS has been compared with other methods of selection. Moll and Stuber (1971) and Moll et al. (1978) reported after eight cycles that yield of the population crosses for 'Jarvis' and 'Indian Chief' increased 1.9 and 3.2% per cycle for full-sib (FS) and RRS, respectively. For the RRS method, Heterosis increased from 19.2% for CO x CO to 27.5% for C6 x C6 and 29.4% for CO x CO to 40.7% for C8 x C8 hybrids (Moll et al., 1978). A change in response to selection after 10 cycles was observed for both selection procedures. Average full-sib selection responses per cycle were 3.5 and 1.4% for the two populations and 2.0% for the population cross. Average RRS responses per cycle were 2.4 and -0.3% for the two populations and 2.7% for the population cross (Moll and Hanson, 1984). Darrah et al. (1972) reported a 7.4% per cycle gain in yield after three cycles of RRS. Eberhart et al. (1973) reported a linear rate of gain of 273 kg/ha (6%) per cycle in grain yield improvement of the population cross of BSSS and BSCB1 after five cycles of RRS. No improvement in grain yield was realized in the BSSS and BSCB1 populations themselves. Martin and Hallauer (1980) reported that, after seven cycles of RRS, grain yield of the BSSS(R) x BSCB1(R) crosses increased 175 kg/ha (3%) per cycle, but yield of the parental populations did not change significantly. Heterosis increased from 14.9% for the CO x CO to 41.7% for C7 x C7. The evidence suggests that heterosis increases markedly with selection for improvement of a hybrid population, such as recurrent selection for SCA or RRS.

To acquire information on the relative importance of partial to complete dominance versus overdominance in yield heterosis, Sprague and Miller (1950) suggested a method to determine the relative importance of dominance and overdominance. To test for the direction of change in gene frequency of two populations, A and B, recurrent selection is carried out in each population using a common inbred tester. They indicated that if dominant and partially dominant gene action effects were of major importance, the intercrosses between A0 x B0, A1 x B1, A2 x B2, etc., should show an upward trend of yield heterosis. However, if overdominance were of major relevance, the two populations should become more alike genetically and intercrosses between selected populations should exhibit a decreasing yield trend as selection progresses.

To test this theory, two studies were carried out. Russell et al. (1973) evaluated populations which had been developed from five cycles of recurrent selection for SCA for yield with the inbred tester B14 in two populations, the open-pollinated variety 'Alph' and the F_2 of (WF9 x B7), by using B14 and BSBB as testers. They found an average yield increase of 309 kg/ha (5%) per cycle in Alph and 132 kg/ha (2%) per cycle in (WF9 x B7) using B14 as a tester and a gain of 363 kg/ha (6%) per cycle in Alph and 151 kg/ha (2.4%) per cycle in (WF9 x B7) using the broad-based tester BSBB. The rates of gain per cycle were significant in all types of populations, being greater in Alph than in WF9 x B7. They concluded that overdominance and overdominant types of epistasis were relatively unimportant in the changes in yield potential of the two populations.

Similar results were reported by Walejko and Russell (1977). In this study two open-pollinated varieties ('Kolkmeier' and 'Lancaster') were used with a common inbred tester, Hy. Progress after five cycles was evaluated in five environments by measuring yields of the populations per se, Hy x Kolkmeier Cn and Hy x Lancaster Cn testcrosses, the Kolkmeier Cn x Lancaster Cn population crosses, and the C0 and C5 populations of both varieties in crosses with Alph C0, Alph C5, B14, B73, and M17. No trend was encountered in Kolkmeier, but yield decreased slightly in Lancaster. However, in the interpopulation cross series, the C5 x C5 combination was significantly higher-yielding than C0 x C0. The authors concluded that dominance, rather than overdominance, was the major type of gene action taking place, and that the use of an inbred line tester seems to be an efficient method to improve breeding populations.

Rojas and Sprague (1952) found that dominance and epistatic variances were more important than additive effects after they made comparisons of variance components in corn yield trials using selected lines. Matzinger et al. (1959) reported on a diallel experiment involving S_1 lines considered to be unselected for yield and concluded that dominance effects were generally larger than additive effects. However, they suggested that considerable upward bias in the former was caused by genotype by environment interactions. Robinson et al. (1949) and Gardner et al.

(1953) obtained estimates of the degree of dominance in the overdominance range for yield genes in F_2 populations. However, later studies by Gardner (1963), Moll et al. (1964), and Moll and Robinson (1967) showed that these estimates of overdominance were due to linkage disequilibrium. Eberhart et al. (1966) demonstrated that additive gene action made up the major portion of the genetic variance for seven characteristics studied in the two open-pollinated varieties, 'Jarvis' and 'Indian Chief.' Dominance effects were relatively larger for yield than for the other characteristics, especially in the variety Jarvis. Epistasis did not contribute significantly to the total genetic effects. Russell (1971), using the inbred Hy and three marker genes (br2, rf1, and wx) obtained comparable results. The frequency of significant additive and dominance effects at individual loci and epistatic effects among loci were greater for all traits in the Hy series than in the B14 series. These results indicated the presence of overdominance or pseudo-overdominance (caused by closely linked genes in repulsion phase) and certain types of epistasis, but were valid for only the specific genotypes studied.

Stuber and Moll (1969) studied F_1 crosses and S_1 progenies from each F_1 in a design II experiment. The pooled analysis showed that no more than 10% of the total genetic variability could be accounted for by epistasis. Thompson et al. (1971) indicated that additive and dominance gene action were responsible for an average of 90% of the variability in the inheritance of ear height.

Moll et al. (1978) compared yield response and heterosis under full-sib family and reciprocal recurrent selection systems. In the full-sib family series, significant improvement in yield was obtained during the successive cycles with little or no change in heterosis. In the reciprocal recurrent series, yield increases were also obtained with a substantial increase in heterosis. Again the authors concluded that the results from both selection series can be accounted for adequately by the assumption of complete dominance.

In general, the results obtained by Lonnquist and Gardner (1961), Gardner (1963), Moll and Robinson (1967), Russell and Eberhart (1975), Sprague and Eberhart (1977), Hallauer (1984), and Horner (1985) indicate that in maize the gene action of most important traits is due mainly to additive genetic effects. Non-additive effects due to dominance rank second with epistasis effects being of least importance. Studies have shown that additive and dominance gene effects are generally much greater than other types of gene effects. Additive effects are precisely those which respond to selection. Thus, as far as the maize breeder is concerned, a practical solution to the dominance-over-dominance disagreement has been reached with the model of additive and dominance effects for heterosis (Sprague, 1983).

Comparison of S_1, S_2, and Testcross Progeny Methods

Many different maize breeding methods have been used successfully, but only a few reports have been published in which direct comparisons were made of relative effectiveness with alternative methods (Horner, 1985).

Comstock (1964) and Wright (1980) indicated that for loci with no overdominance, selection among S_1 progenies should be about twice as effective as testcross evaluation for changing gene frequencies in a population.

Smith (1986) evaluated the possible reasons for the low values, reported in the literature, for the relationship between line per se and testcross performance. By computer simulation he showed that, for traits conditioned by a large number of loci showing complete dominance, the correlation between line per se and testcross performance is expected to be less than 0.5. This is due to the masking effects of favorable dominant alleles in the tester. Thus, this result agrees with previous reports which indicated that the use of a high performance tester will decrease the genetic variance.

Selfed progeny selection utilizes fundamentally additive and partial to complete dominance gene action. The procedure includes evaluation of S_1 or S_2 lines per se and selection of the highest yielding ones for intercrossing to initiate a new cycle. Half-sib progeny (testcross method) selection utilizes additive gene action when the population is used as a tester (Sprague et al., 1959; Penny et al., 1962; Russell et al., 1973; and Horner et al., 1973). It has been reported that genetic variance is, as expected, greater among selfed progenies than among testcross progenies under similar environmental conditions (Darrah et al., 1972; Horner et al., 1973).

The first evaluation of S_1 and S_2 line selection was made by Davis (1934) in which lines were selfed for two generations, then crossed with an unrelated open-pollinated variety tester. He found that the average yield of S_1 and S_2 lines was more reliable than that of testcrosses for selection

Genter and Alexander (1962) made comparative performance tests between S_1 lines selected on the basis of S_1 progeny yield and S_1 lines selected on the basis of testcross performance with single-cross testers. They reported more dispersed means (larger variance) and fewer environmental effects from S_1 progenies than from testcrosses. After two cycles of selection, Genter and Alexander (1966) found that inbred lines obtained from S_1 progeny population showed a yield increase of 31.4%. However, only a 17.9% yield increase was obtained using the testcross method with the parental population as the tester. The more productive S_1 lines tended to produce the more productive crosses, but the correlation between S_1 line and testcross yield decreased from 0.61% to 0.15% from the first to the second cycle of selection. Genter and Alexander did not report combining ability for the studied populations.

Koble and Rinke (1963) compared random S_1 progenies and testcrosses with related and unrelated population testers.

They concluded that the S_1 selection method could replace the testcross selection method. Lonnquist and Lindsey (1964) and Lonnquist and Castro (1967) reported that the S_1 progeny method seems to be a more logical procedure in the preliminary selection of desirable parents than the testcross methods with related and unrelated testers. Duclos and Crane (1968) reported that a significant increase in yield was made in one cycle by both S_1 progeny selection and selection for combining ability with an unrelated double-cross tester. However, there was no further increase from a second cycle of selection with either method. Torregroza and Harpstead (1965) found that over different environments S_1 progeny selection was more effective than testcross selection with related and unrelated population testers.

da Silva and Lonnquist (1968) compared two methods of population improvement and found that there was good agreement between observed and expected selection response for full-sib family selection and S_1 testcross progeny selection. They indicated that with equal selection intensity, S_1 testcross progeny selection is expected to be at least as effective as full-sib family selection. Lonnquist (1968) reported a 15%, 4%, and 0% gain in the yield of synthetics, when they were developed by intercrossing the selected lines on the basis of the parental population tester, S_1 progeny test, and an unrelated population tester, respectively. Caranjal et al. (1971) reported 4.6% improvement with the S_1 selection method and 2.7% improvement with the testcross method for grain yield. However, the two methods were equally effective for improvement of GCA. Harris et al. (1972) evaluated S_1 lines themselves and in testcross performance after nine cycles of mass selection for yield in irradiated and non-irradiated 'Hays Golden'. They showed that S_1 lines from the selected populations were superior in mean yield to lines of the parent variety either as S_1 lines themselves or in test- crosses. It was concluded that selection eliminated radiation-induced deleterious mutants from the irradiated population while increasing frequencies of favorable yield genes common to both selected populations. Genter (1973) found that S_1 progeny selection was slightly better for improving yields of synthetics, but there was no difference between methods for combining ability with unrelated testers. However, Genter and Eberhart (1974) reported that the two methods were essentially equal with respect to both yield of synthetics and combining ability with unrelated testers. Goulas and Lonnquist (1977) found that on the basis of two cycles of selection the S_1 progeny procedure was about equal to a combination of half-sib and S_1 progeny evaluation.

Darrah et al. (1972, 1978) compared on the basis of two cycles several different recurrent selection methods in three populations, and found no improvement with S_1 selection and testcross progeny methods. Inbreeding and lack of linkage equilibrium in 'Kitale Composite A' were reported as contributing. In a computer simulation study Choo and Kannenberg (1979) found that the S_1 selection method for population improvement was more efficient than mass and modified ear-to-row selection. Smith (1979), using a modified diallel analysis for evaluating improvement for recurrent selection, showed that half-sib and S_1 selection increased the frequencies of alleles with additive effects and that S_1 selection was more efficient than half-sib selection. Also he indicated that the rate of inbreeding depression was equal for the two methods. West et al. (1980) reported that S_1 progeny selection was more effective for yield than reciprocal full-sib selection; however, the two methods were equal in improvement of the variety cross.

In comparing full-sib, half-sib, and S_1 selection methods after one cycle of selection, Mukherjee et al. (1980) found that the S_1 selection method was the most effective method for improving yield in four populations. Similarly, Moll and Smith (1981) indicated that, after five cycles, response to the S_1 progeny selection method was approximately 50% greater than response to full-sib family selection. Burton et al. (1971) reported that after four cycles of recurrent selection, both the mean yield and GCA of synthetics were significantly improved and that the S_1 progeny method was more effective than the double-cross tester method. In the same experiment after eight cycles of half-sib family and S_1 progeny recurrent selection, Tanner (1984) reported no significant difference between methods for yield of populations per se or for combining ability of the selected C8 populations.

Horner (1963) compared S_0 plants (S_1 lines) with S_1 plants (S_2 lines) for GCA and concluded that more progress could be made with S_1 plants. The variance component estimate for crosses involving S_1 plants was larger than the estimate for crosses of S_1 lines. He indicated that subsequent selfings do provide an opportunity to identify superior genotypes. From work with computer simulations, Cress (1967) suggested testing S_1 plants (essentially S_2 lines) rather than S_0 plants (S_1 lines) as a means for more rapid gain in recurrent selection programs.

Horner (1968) pointed out that "for a single locus with two alleles, crossing S_1 rather than S_0 plants with a tester is expected to increase variance among test crosses within intercross progenies (of selected S_1 lines from the previous cycle) by 100%, and over the entire population by 50%" (32). He reported that when S_1 lines were intercrossed a generation of sib-pollination within intercross progenies increased the estimate of testcross variance from 0.046 to 0.141 where an increase of 50% was expected. Where S_2 lines were intercrossed, a generation of inbreeding increased test cross variance from 0 to 0.172. He concluded that a generation of sib-pollination prior to initiation of a new cycle would be an effective step in breeding programs.

On the basis of results by Darrah et al. (1972) and Horner et al. (1973) that genetic variance among testcross progenies using inbred testers was about twice as large as when broad-base testers were used, Russell and Eberhart

(1975) proposed a modified reciprocal recurrent selection scheme using inbred testers instead of the populations themselves as a means of utilizing additive genetic variance. However, Comstock (1979) indicated that in theory the populations are expected to be slightly superior to inbred lines as testers for changing allele frequency, even though the latter result in larger genetic variances among progenies. Horner et al. (1969) compared narrow and broad base testers as well as S_2 progeny method after three cycles of selection. They concluded that the S_2 progeny method was as effective as the parental tester method for population improvement and suggested that the former places more emphasis on contributions of homozygous loci than heterozygous loci. The parental tester method produced the highest yielding random-mated (Syn-3) population, and the S_2 progeny method produced the highest yielding selfed population. Horner et al. (1973), from two additional cycles, obtained a significant linear increase in general combining ability over cycles for all methods, but selection based on yield of S_2 progenies was less effective than the inbred tester method for improving combining ability. However, the S_2 method was just as effective as use of the parental population as the tester. Inbreeding depression was higher in populations developed by the two testcross methods than in the S_2 progeny method. Thus, the S_2 progeny method is more effective in decreasing the frequency of recessive deleterious genes, which should result in more vigorous homozygous lines.

In a later experiment Horner et al. (1977) found that after one cycle of selection there were no significant differences between the S_2 line selection method and the testcross method. Baniya (1982), in a continuation of the same experiment, reported that after two cycles of selection, each method was effective in improving grain yield of populations per se and yield of interpopulation crosses, but there was no significant difference between them. If the goal is to improve combining ability the testcross method was more effective than the S_2 progeny method. Gains per cycle for combining ability with the inbred testers were 6.8% and 3.8% for the testcross and the S_2 progeny method, respectively. Jensen et al. (1983) reported that S_2 testcrosses are superior to S_2 per se tests when selecting for combining ability. They suggested that most of exploitable genetic variation in their elite materials was probably non-additive. After three cycles, however, Horner (1985) again, as in the first cycle, found no significant difference betwwen S_2 and testcross methods for combining ability improvement. Nevertheless, S_2 selection resulted in markedly better yield of inbred lines than the testcross method. He suggested that genetic variation for yield in corn is largely additive. However, some non-additive variation in the overdominance range at some loci is possible. Clucas (1985) evaluated 400 S_2 lines and their respective testcrosses in three environments in Iowa. He found that the mean grain yield and stand percentage of the visually selected lines were 169 kg/ha and 2.58% greater, respectively, than those of the randomly selected lines. No significant differences were observed between means of testcross progenies of visually and randomly selected lines. Correlations between S_1 line traits and the same traits in testcrosses were 0.19, 0.59, 0.51, 0.48, and 0.29 for grain yield, grain moisture content, stalk lodging, root lodging, and vertical root-pull resistance, respectively. He concluded that selection for superior testcross performance based on S_2 performance per se is not practical.

In summary, this review yields the following conclusions regarding gene action, and selfed progeny versus testcross methods:

a. Collectively these studies showed that in some instances overdominance and epistasis can be detected, but in general, heterosis in maize seems primarily due to additive genetic effects with partial to complete dominance.

b. The findings do not suggest any marked differences in efficiency between the two methods of selection.

c. Further comparison of these two methods of selection will be required before conclusions can be drawn.

MATERIALS AND METHODS

Source of Materials

Two populations, A and B, were derived from a wide-base maize synthetic, FSHmR, which was developed at the University of Florida for resistance to the fungus *Helminthosporium maydis* N. and M. About 400 S_2 lines from each population were grown in 1975, and about 200 lines of each group were selected on the basis of plant vigor and disease resistance. Each of the 200 lines was sibbed and crossed with an inbred (S_1) tester from the other population for combining ability evaluation. For further evaluation 109 and 102 lines from Populations A and B, respectively, were chosen. These lines were evaluated by Robinson (1976) for combining ability with an S_1 line tester and for performance of S_2 lines per se. Horner et al. (1977), Baniya (1982), and Horner (1985) also evaluated progress in this experiment after one, two, and three cycles of selection, respectively. The experiments reported in this study utilize these materials after three cycles of selection.

Experiment I: Effect of Breeding Method on Combining Ability of Third-Cycle Lines.

Ten selected third-cycle lines from each population (Table 1) were grown at the University of Florida in Gainesville during 1985 in adequate quantities to make

Table 1. Entries used in the factorial cross.

Population A	Population B
3AT3 (92514-1 selfed)	3BT1 (92891-1 selfed)
3AT6 (92547-1 selfed)	3BT2 (92903-1 selfed)
3AT10 (92628-1 selfed)	3BT5 (92959-1 selfed)
3AT15 (92762-1 selfed)	3BT8 (93014-1 selfed)
2AT98-2-1 (00281-1 selfed)	2BT40 (40051-1 selfed)
3AS2 (10222-1 selfed)	3BS1 (10415-1 selfed)
3AS3 (10243-1 selfed)	3BS2 (10446-1 selfed)
3AS6 (10275-1 selfed)	3BS5 (10484-1 selfed)
3AS12 (10332-1 selfed)	3BS6 (10486-1 selfed)
3AS15 (10394-1 selfed)	3BS7 (10488-1 selfed)

intercrosses in a factorial mating design. Lines with an "S" in the name were from the S_2 progeny method and those with a "T" were from the testcross method. Each of the 10 parents in Population A was crossed to each of the 10 parents in Population B. This resulted in 100 crosses excluding reciprocals. Making the crosses involved collecting pollen from 8 to 12 plants of each parent from Population A and bulking the pollen before applying it to 8 to 12 plants of each of the 10 parents in Population B. Pollen from plants of parents in Population B was handled likewise. Some of the parents were grown again in Gainesville during the fall of 1985 in order to repeat crosses that failed to produce enough seed due to high summer temperatures. After harvest and drying, the ears from each cross were shelled and the seed was bulked to produce one seed lot for each cross.

The 100 crosses were tested in one-row plots at two locations with different soil types near Gainesville, Florida, in 1986, using a randomized complete block design (RCBD) with nine replications at each location. Row spacing was 91 cm and the plants were spaced 30.5 cm apart in the rows. Two seeds were planted per hill and the plants were thinned to one per hill at the seedling stage. After thinning there was a maximum of 20 plants per plot at both locations. A purple stalk hybrid was used for border rows. Fertilization was according to recommended rates for the area. Weeds were controlled with a preplant incorporated application of atrazine and Sutan plus, as well as some cultivations.

Irrigation and insecticides were applied when required for proper growth.

Data were recorded for grain yield per plot, average ear height, percentage two-eared plants, mean husk score, percentage erect plants at harvest, and ear (grain) quality. Ear height was measured, on a plant that represented the average ear height in the plot, from ground level to the node of attachment of the highest ear. Husk score was determined on a scale of one (best) to nine (worst), depending upon the extension and tightness of the husk. Extended, tight husks are more desirable. Grain quality (rotten kernels) scores were determined on a scale of one (best) to nine (worst). All plants broken below the ear or bent more than 30 degrees were counted as non-erect. A one-row plot combine was used for harvest, with care taken to pick up lodged plants. Yield was measured in megagrams of grain per hectare adjusted to 15% moisture before analysis.

The analysis of variance (Table 2) for each trait was performed on the assumption that the effects were random in order to compare the relative importance of GCA and SCA. The analysis was based on the following model:

$$Y_{ijk} = u + L_j + R_{k(j)} + C_i + (CL)_{ij} + E_{ijk}$$

where Y_{ijk} is the mean response associated with ith cross of the jth location in the kth replication;

u is the overall mean;

L_j is the effect of the jth location, j = 1, 2;

Table 2. Expected mean squares for GCA and SCA.

Source of variation	df	EMS
Locations (L)	1	
Reps / L	16	
Crosses (C)	99	$\sigma^2 + r\sigma^2abl + r\sigma^2lc + rl\sigma^2c$
A parent	9	$\sigma^2 + r\sigma^2abl + ra\sigma^2bl + rl\sigma^2ab + rlb\sigma^2a$
B parent	9	$\sigma^2 + r\sigma^2abl + rb\sigma^2al + rl\sigma^2ab + rla\sigma^2b$
A X B	81	$\sigma^2 + r\sigma^2abl + rl\sigma^2ab$
C X L	99	$\sigma^2 + r\sigma^2abl + r\sigma^2lc$
A X L	9	$\sigma^2 + r\sigma^2abl + rb\sigma^2al$
B X L	9	$\sigma^2 + r\sigma^2abl + ra\sigma^2bl$
(A X B) X L	81	$\sigma^2 + r\sigma^2abl$
Error	1584	σ^2
Total	1799	

σ^2 is the error variance, and l, r, a, b, and c refer to the number of locations, replications, lines from Population A and B, and crosses, respectively.

$R_{k(j)}$ is the effect of the kth replication in the jth location, k = 1, 2,...,9;

C_i is the effect of the ith cross, i = 1, 2,...,100;

$CL_{(ij)}$ is the interaction effect of the ith cross and the jth location; and

E_{ijkl} is the error term of the ith cross of the jth location in the kth replication; it includes all other possible sources of variation.

To estimate GCA and SCA effects, the crosses sums of squares were partitioned into sources of variation due to crosses of the 10 A parents, the 10 B parents, and A x B interaction. The crosses (C) and locations (L) sums of squares were similarly partitioned into A x L, B x L, and (A x B) x L sources.

Experiment II: Determination of Inbreeding Depression

After screening of about 400 third-cycle lines for desirable agronomic traits, between 100 and 125 lines were evaluated at two locations with five replications at each location for each population (A and B) and method (selfed and testcross progeny). Thirteen to fifteen of the better-performing parental lines for the traits studied from each of the four populations were chosen for recombination. These selected lines were intercrossed (by hand) within populations in order to get maximum heterozygosity. Four first-generation synthetics (Syn-1) were obtained by bulking equal numbers of seed from all crosses within populations and methods.

To determine the effects of selection method on yield of inbred generations, each of the four third-cycle populations was sampled by advancing 100 random S_1 lines to S_2's by selfing. Equal numbers of seed from each population and method were bulked to form four S_1 and four S_2 bullks. These composites, along with Syn-1 bulks, were tested at two locations near Gainesville, Florida, in 1985 and 1986. Eight replications were grown each year at each location. One-row plots with 20 plants per row were planted at the rate of 36,000 plants per hectare. A split-plot design with borders between generations was used to compare the Syn-1 (S_0) generation with random S_1 and S_2 bulks of the third-cycle populations. The Syn-1, S_1, and S_2 were main plots and the four composites were subplots. The less important treatment effects were allocated to the whole plots and the more important treatment effects to the subplots in order to obtain the maximum precision where it is most desired. The main plots were assigned to each block at random and the subplots were randomized within main plots.

Data on grain yield per plot, ear height, mean husk score, ear weight, and percentage of erect plants at harvest were taken prior to harvesting. The plots were harvested by hand and total number of ears and field weight to the nearest tenth pound were recorded. Ten good representative ears from three replications at each location were saved, dried to about 12% moisture, and shelled for dry grain determinations.

Prior to statistical analysis, the yield was adjusted to full stand by multiplying the yield at harvest by the ratio of number of plants at full stand to the number of plants harvested. The factors used for each missing plant were calculated to decrease yield disadvantage that a plot with a poor stand might have compared with those plots with full stands. Finally, the field weight of each plot was converted to kilograms and adjusted for moisture and shelling percentage by multiplying the field weight by average percentage of dry grain recovery for each entry.

The average coefficient of inbreeding was calculated for each generation (Syn-1, S_1, and S_2).

The data were first analyzed as a split-plot design to compare generations for each trait and then as a randomized complete block design at each of the three levels of inbreeding to compare methods and populations (Table 3). When significant differences were found among traits, least significant difference (LSD) was employed to separate means. The analysis was based on the following model:

$Y_{ijk} = u + A_i + B_{j(i)} + C_k + CA_{(ki)} + E_{ijk}$

where u is the overall mean;

A_i is the effect of the ith environment, $i = 1,\ldots,4$;

$B_{j(i)}$ is the effect of the jth replication in the ith environment, $j = 1,\ldots,8$;

C_k is the effect of the kth composite, $k = 1,\ldots,4$;

Table 3. Combined analyses of variance for several traits of Syn-1, S_1, and S_2 generations (separate analyses).

Source of variation	df	EMS
Environments (E)	3	
Reps / E	28	
Composites (C)	3	$\sigma^2 + r\sigma^2_{emp} + r\sigma^2_{ec} + re\sigma^2_{c}$
Methods (M)	1	$\sigma^2 + r\sigma^2_{emp} + rm\sigma^2_{pe} + re\sigma^2_{mp} + rep\sigma^2_{m}$
Populations (P)	1	$\sigma^2 + r\sigma^2_{emp} + rp\sigma^2_{me} + re\sigma^2_{mp} + rem\sigma^2_{p}$
M x P	1	$\sigma^2 + r\sigma^2_{emp} + re\sigma^2_{mp}$
E x C	9	$\sigma^2 + r\sigma^2_{emp} + r\sigma^2_{ec}$
E x M	3	$\sigma^2 + r\sigma^2_{emp} + rp\sigma^2_{me}$
E x P	3	$\sigma^2 + r\sigma^2_{emp} + rm\sigma^2_{pe}$
E x (M x P)	3	$\sigma^2 + r\sigma^2_{emp}$
Error	84	σ^2
Total	127	

$CA_{(ki)}$ is the interaction effect of the kth composite and ith environment; and

E_{ijk} is the error term of the ith environment of the jth replication in the kth composite.

To estimate method and population effects, the sums of squares for composites were partitioned into sources of variation attributed to methods, populations, and the interaction between methods (M) and populations (P). The composites (C) and environments (E) sums of squares were similarly partitioned into E x M, E x P, and (M x P) x E sources.

Experiment III: Yield of Selected C4 Lines from Each Population and Method

To determine the effect of breeding methods on vigor of selected inbred lines derived from cycle 4 populations, four composites were obtained by bulking equal amounts of seed from the selected fourth cycle S_2 lines of each population and method (Table 4). The four composites were evaluated in one-row plots in 1986 at two locations near Gainesville, Florida. A randomized complete block design (RCBD) with ten replications was used at each location. Row-to-row spacing was 91 cm and plant-to-plant distance in the row was 30.5 cm. Two seeds were planted per hill and the plants were thinned to one per hill when they had reached 15-cm height. After thinning, there was a maximum of 20 plants per plot at both locations.

Table 4. Cycle 4 lines from each population and method used in vigor evaluations.

S_2 progeny method (S_2)		Testcross method (TC)	
Pop. A	Pop. B	Pop. A	Pop. B
40193	40375	30360	30686
40212	40385	30422	30707
40227	40402	30440	30743
40250	40412	30442	30782
40256	40417	30462	30807
40258	40431	30468	30829
40262	40437	30495	30849
40279	40448	31492	31821
40280	40454	31476	31824
40286	40459	31583	31829
40304	40474	31617	31884
40319	40484	31628	31977
40320	40486	31674	-
40321	40498	31697	-
40340	40512	31748	-
40348	-	-	-
40357	-	-	-

Data on grain yield per plot, ear height, husk score, and percentage of erect plants at harvest were taken prior to harvesting. The plots were harvested by hand, and total number of ears and field weight per plot were registered. Representative ears from four replications were saved, dried, and shelled for dry matter calculations. The field weight of each plot was adjusted to Mg/ha shelled grain at 15% moisture and full stand. The analysis of variance (Table 5) was performed for adjusted grain yield, ear height, ears per plant, husk score, ear weight, and percentage of erect plants at harvest.

The appropriate statistical model is given below:

$Y_{ijk} = u + A_i + B_{j(i)} + C_k + CA_{(ki)} + E_{ijk}$

where u is the overall mean;

A_i is the effect of the ith location, i = 1, 2;

$B_{j(i)}$ is the effect of the jth replication in the ith location, j = 1,...,10;

C_k is the effect of the kth composite, k = 1,...,4;

$CA_{(ki)}$ is the interaction effect of the kth composite and the ith location; and

E_{ijk} is the error term of the ith location of the jth replication in the kth composite.

To estimate method and population effects, the sums of squares for composites were partitioned into sources of variation attributed to methods, populations, and the interaction between methods (M) and populations (P). Similarly, the sums of squares for composites (C) and

Table 5. Partitioning of variance and expected mean squares used in analyses of several traits of the four selected fourth-cycle Populations.

Source of variation	df	EMS
Locations (L)	1	
Reps / (L)	18	
Composites (C)	3	$\sigma^2 + r\sigma^2lmp + r\sigma^2lc + rl\sigma^2c$
Methods (M)	1	$\sigma^2 + r\sigma^2lmp + rm\sigma^2pl + rl\sigma^2mp + rlp\sigma^2m$
Populations (P)	1	$\sigma^2 + r\sigma^2lmp + rp\sigma^2ml + rl\sigma^2mp + rlm\sigma^2p$
M x P	1	$\sigma^2 + r\sigma^2lmp + rl\sigma^2mp$
L x C	3	$\sigma^2 + r\sigma^2lmp + r\sigma^2lc$
L x M	1	$\sigma^2 + r\sigma^2lmp + rp\sigma^2ml$
L x P	1	$\sigma^2 + r\sigma^2lmp + rm\sigma^2pl$
L x (M x P)	1	$\sigma^2 + r\sigma^2lmp$
Error	54	σ^2
Total	79	

locations (L) were partitioned into L x M, L x P, and (M x P) x L sources.

Experiment IV: Correlation of Inbred Lines (S_2 Parents) and Testcross Performance

S_2 lines for the S_2 progeny method were obtained by saving only one selfed ear from each parental S_1 line. Two hundred seventy-eight inbred lines from Populations A and B were grown in two replications at one location near Gainesville, Florida, in 1984. Row-to-row spacing was 91 cm and plant-to-plant distance in the row was 30.5 cm. About 15 plants per plot were maintained. Standard agronomic practices were used including irrigation and insect control when needed. During the growing period stalk quality, ear height, husk score, and ears per plant were recorded for each line. Stalk quality and husk score were determined on a scale from 1 (best) to 9 (worst). Ear height was measured from the ground to the node of attachment of the highest ear. The plots were hand harvested, and the lines were evaluated for ear quality on a scale from 1 to 5.

In a parallel test, the same S_2 lines were evaluated for performance of their testcrosses using inbred testers. An S_3 line from Population A was used as a tester to evaluate lines from Population B and vice versa. These testcrosses were evaluated at two locations near Gainesville, Florida, in 1984. About 25 plants were maintained per plot. A randomized complete block design (RCBD) with five replications at each location was used to evaluate testcross performance. A plot combine was used for harvest.

Correlations were calculated using entry means over two environments for the testcrosses and means from one environment for the S_2 lines. Simple correlation coefficients of the means for five traits observed in 1984 were calculated to determine the relationship between S_2 parents and testcross traits.

RESULTS AND DISCUSSION

Experiment I. Effect of Breeding Method on Combining Ability of Third-Cycle Lines

Variation among the 100 crosses was significant ($P<0.01$) for all traits studied (Table 6). Interaction between crosses and locations was also significant at the 0.01 level for all traits except ear height, which showed significance only at the 0.05 level. Variation for general combining ability (GCA) among parents was significant ($P<0.01$) in both populations for all traits. Except for ear height in Population A, GCA x location interactions were also significant ($P<0.01$) for all traits.

In Parental Group A the inbred tester method was superior ($P<0.01$) on the basis of all crosses to the S_2 progeny method for grain yield, ear height, and husk score. Mean differences for these traits were, respectively, 0.26 Mg/ha (4%), 3.6 cm (3%), and 1.0 (19%). In Parental Group B, the inbred tester method was superior at the 0.05 level for grain yield (0.14 Mg/ha or 2%) and at the 0.01 level for ear height (4%), two-eared plants (15%), erect plants (9%), and husk score (7%) (Tables 6 and 7). On the basis of means of the 25 crosses obtained by crossing the 3AS with the 3BS lines compared with the 25 3AT by 3BT crosses, the inbred tester method was superior by an even larger margin for all traits (Table 7, last column).

There was significant ($P<0.01$) variation within methods in GCA among parents in both parental groups for all traits. As a

Table 6. Combined analyses of varicance for grain yield, ear height, number 2-eared plants, percentage erect plants, and husk score at two locations.

Source of variation	df	Trait				
		Grain yield	Ear height	Two-eared plant	Erect plant	Husk^{+} score
		Mg/ha	cm	no.	%	
Locations (L)	1	244.55**	6598.2**	4439.4**	447966.7**	12.8**
Reps / L	16	34.70**	212.1**	51.4**	2091.0**	9.2**
Crosses (C)	99	4.83**	26.0**	183.6**	3214.9**	29.9**
A parent crosses	9	25.98**	71.1**	994.7**	5887.6**	179.7**
Methods (M)	1	30.04**	156.1**	7.0	714.3	405.4**
Lines / M	8	25.47**	60.5**	1118.2**	6534.3**	151.5**
B parent crosses	9	8.14**	164.4**	684.6**	25088.0**	79.4**
Methods (M)	1	9.75*	331.3**	352.6**	22302.6**	54.4**
Lines / M	8	7.90**	143.5**	726.1**	25436.2**	82.5**
A X B	81	2.12**	5.7	37.8**	487.6**	7.8**
C X L	99	1.14**	6.9*	18.5**	2328.2**	2.3**
A X L	9	2.17**	9.4	65.4**	4294.5**	5.4**
B X L	9	4.06**	17.2**	81.6**	19781.2**	6.1**
(A X B) X L	81	0.71	5.4	6.3	170.5	1.5
Error	1584	0.76	5.1	6.0	213.5	1.3

*, ** significant at the 0.05 and the 0.01 probability levels, respectively.
+ scores were on a 1 (good) to 9 (poor) scale.

Table 7. Comparison of two selection methods for performance of crosses between selected inbred lines in two populations.

Method of selection	Population A Gaines-ville	 Green Acres	 Average
		Grain yield, Mg/ha	
S_2 progeny	5.81	6.55	6.18
Inbred tester	6.07	6.81	6.44
			**
		Ear height, cm	
S_2 progeny	108.7	129.3	119.0
Inbred tester	104.7	126.1	115.4
			**
		Two-eared plants	
S_2 progeny	4.2	7.2	5.7
Inbred tester	3.9	7.2	5.6
			ns
		Erect plants, %	
S_2 progeny	95.2	62.4	78.8
Inbred tester	95.1	65.1	80.1
			ns
		Husk score	
S_2 progeny	6.4	6.4	6.4
Inbred tester	5.3	5.6	5.4
			**

Table 7--continued.

Method of selection	Population B Gaines-ville	 Green Acres	 Average	Mean for all crosses	Mean within$^+$ methods
	Grain yield, Mg/ha				
S_2 progeny	5.87	6.60	6.24	6.21	6.15
Inbred tester	6.01	6.76	6.38	6.41	6.56
			*		
	Ear height, cm				
S_2 progeny	109.2	129.5	119.4	119.2	121.7
Inbred tester	104.3	125.9	115.1	115.2	113.7
			**		
	Two-eared plants				
S_2 progeny	3.8	6.5	5.2	5.4	5.4
Inbred tester	4.2	7.8	6.0	5.8	6.1
			**		
	Erect plants, %				
S_2 progeny	95.4	56.5	76.0	77.4	75.7
Inbred tester	95.0	71.0	83.0	82.0	84.1
			**		
	Husk score				
S_2 progeny	6.1	6.2	6.2	6.3	6.5
Inbred tester	5.6	5.9	5.8	5.6	5.2
			**		

*, ** Means within columns in a group are significantly different at the 0.05 and 0.01 levels, respectively.

+ Means of the 25 crosses ASXBS versus means of the 25 ATXBT lines.

ns nonsignificant

result, a few lines from the S_2 progeny method had combining ability (GCA) as good as the best lines from the inbred tester method (Tables 8-12). For example, line 3AS2 had high GCA values for grain yield and two-eared plants and 3BS1 had a high GCA value for ear height.

Specific combining ability effects (A X B interaction) were significant at the 0.01 level for all traits except ear height (Table 6). These results show that some crosses performed significantly better or worse than expected, based on the GCA values of their parents. No significant difference was detected for interaction of specific combining ability (SCA) effects with locations.

The average performance of a line in a series of crosses is a measure of its GCA, whereas the performance of a specific cross in relation to expected performance based on parental GCA measures the SCA of the two lines being crossed. The results for grain yield (Table 8) show that 3AS2, 3AT15, 2AT98-2-1, and 3AT10 in Parental Group A were good general combiners for grain yield. The rest of the parents except 3AT3 showed negative GCA effects, which suggests that they were below average for this group of parents. The range in GCA effects for the A Group was from -0.46 to +0.64 ±0.26 Mg/ha. In the B Parental Group, 2BT40 and 3BT2 were good general combiners, and 3BS1, 3BT1, and 3BT8 were very close to the average. The range in GCA effects for the B Group was from -0.37 to +0.28 ±0.26 Mg/ha. These data also suggest that the inbred tester method was more effective than the S_2 progeny method for evaluating GCA because more "T" than "S" lines were high in GCA.

Table 8. GCA and SCA effects of the 100 crosses relative to the mean grain yield. The upper number is the mean for the cross and the lower is the SCA effect.

	SCA effects (Mg/ha)											
Parents	3BS1	3BS2	3BS5	3BS6	3BS7	2BT40	3BT1	3BT2	3BT5	3BT8	Standard deviation of SCA effects	GCA effects (Mg/ha)
3AS2	7.05 +0.040	6.42 −0.149	6.93 +0.069	7.21 +0.143	7.40 +0.498	7.44 +0.428	6.70 −0.295	7.13 −0.104	6.19 −0.475	7.08 +0.021	0.28	+0.64
3AS3	6.10 +0.168	5.64 +0.149	5.64 −0.143	5.92 −0.069	6.18 +0.356	5.95 −0.164	6.07 +0.153	6.26 +0.104	5.48 −0.107	5.53 −0.451	0.23	−0.43
3AS6	6.36 +0.222	5.46 −0.237	6.29 +0.301	6.39 +0.195	5.76 −0.270	5.75 −0.570	5.94 −0.183	6.74 +0.378	5.99 +0.197	6.15 −0.037	0.31	−0.23
3AS12	5.78 −0.122	5.46 +0.001	5.80 +0.047	6.58 +0.621	5.76 −0.034	5.22 −0.864	6.59 +0.703	6.10 −0.026	5.32 −0.237	5.86 −0.091	0.44	−0.46
3AS15	6.33 +0.126	5.66 −0.103	5.96 −0.095	5.92 −0.341	5.88 −0.216	6.16 −0.226	6.82 +0.631	6.28 −0.148	5.90 +0.041	6.58 +0.327	0.29	−0.16
3AT3	6.96 +0.552	5.98 +0.013	5.74 −0.519	6.37 −0.095	6.34 +0.040	6.66 +0.070	6.29 −0.103	6.74 +0.108	6.00 −0.063	6.45 −0.007	0.26	+0.04
3AT6	6.08 +0.037	5.51 −0.092	5.87 −0.024	6.16 +0.060	5.54 −0.395	6.72 +0.495	6.14 +0.112	6.10 −0.167	5.38 −0.318	6.38 +0.288	0.27	−0.32
3AT15	6.28 −0.396	6.40 +0.165	6.64 +0.113	6.96 +0.227	6.68 +0.112	6.96 +0.102	6.42 −0.241	7.00 +0.010	6.44 +0.109	6.46 −0.265	0.21	+0.31
2AT98-2-1	5.96 −0.779	6.55 +0.252	6.78 +0.190	6.26 −0.536	6.35 −0.281	7.53 +0.609	6.50 −0.224	7.06 +0.097	6.43 +0.036	7.42 +0.632	0.46	+0.37
3AT10	6.76 +0.151	6.17 +0.002	6.52 +0.060	6.46 −0.206	6.69 +0.189	7.09 +0.299	6.04 −0.554	6.49 −0.343	7.08 +0.816	6.24 −0.418	0.40	+0.24
Standard deviation of SCA effects	0.37	0.15	0.22	0.33	0.29	0.46	0.40	0.20	0.35	0.34		
GCA effects	+0.06	−0.37	−0.09	+0.11	−0.05	+0.24	+0.04	+0.28	−0.29	+0.10		

S.E. GCA = 0.26 Mg/ha
S.E. SCA = 0.78 Mg/ha

The results for ear height (Table 9) indicate that one line from the S_2 progeny method (3AS6) and four lines from the testcross method (3AT6, 3AT15, 2AT98-2-1, and 3AT10) in the A Group had good combining ability for ear height because they had negative GCA effects (negative GCA effects are more desirable for ear height than positive GCA effects because short plants are desired). Lines 3AT15, 2AT98-2-1, and 3AT10 also showed good combining ability for grain yield (Table 8). In the B Group, one line from the S_2 progeny method (3BS1) and four lines from the inbred tester method (2BT40, 3BT1, 3BT5, and 3BT8) were good combiners for ear height; their GCA effects were significantly different from zero. The ranges in ear height GCA effects were -5.11 to +5.06 ±0.68 cm and -6.74 to +11.03 ± 0.68 cm for Parental Groups A and B, respectively.

The results for two-eared plants (Table 10) indicate that 3AS2 and 2AT98-2-1 in Parental Group A were good combiners; the rest had nearly zero or negative GCA effects, showing that they were below the average for this set of parents. Again the testcross method was superior to the S_2 progeny method for the A Group. The range in GCA effects was from -4.26 to +3.76 ±0.74. In the B Parental Group, line 3BT2 had the best GCA value (+3.91) for two-eared plants of all 10 lines. The rest had GCA values close to zero or negative. The range in GCA effects for the B Group was from -3.42 to +3.91 ±0.74.

General combining ability effects for erect plants at harvest are shown in Table 11. In the A Parental Group, 3AS2,

Table 9. GCA and SCA effects of the 100 crosses relative to the mean ear height. The upper number is the mean for the cross and the lower is the SCA effect.

	SCA effects (cm)											
Parents	3BS1	3BS2	3BS5	3BS6	3BS7	2BT40	3BT1	3BT2	3BT5	3BT8	Standard deviation of SCA effects	GCA effects (cm)
3AS2	116 +0.21	122 -1.51	130 -3.26	127 +2.16	126 +1.89	121 +2.62	116 -0.57	124 -0.75	115 -4.21	123 +3.40	2.54	+4.84
3AS3	111 -0.77	120 -0.21	126 -3.26	121 -0.04	118 -2.11	118 +2.62	114 +1.32	126 +4.35	117 +0.99	113 -2.90	2.42	+1.04
3AS6	103 -5.41	117 +0.27	126 +0.52	120 +2.44	118 +0.57	105 -6.50	109 +0.10	121 +3.03	116 +3.87	114 +1.28	3.40	-2.44
3AS12	114 +2.67	121 +1.25	132 +3.20	120 +0.22	126 +6.35	114 -0.82	108 -3.52	118 -3.39	115 +0.05	110 -6.04	3.66	+0.58
3AS15	117 +1.29	120 -3.83	140 +6.72	124 -0.66	127 +2.47	116 -2.60	116 -0.40	125 -0.47	118 +1.63	119 -0.92	2.96	+5.06
3AT3	116 +3.28	122 +0.76	125 -5.49	123 +0.93	121 -0.54	118 +1.79	112 -1.11	125 +2.12	114 -3.34	119 +1.57	2.69	+2.27
3AT6	108 +2.26	114 +0.14	119 -4.21	116 +1.11	113 -1.56	105 -3.43	111 +5.17	111 -3.90	112 +2.34	112 +2.05	3.16	-5.11
3AT15	108 -1.62	118 +0.26	133 +5.51	119 -0.47	113 -0.54	116 +2.19	110 -0.81	119 -1.08	109 -5.64	117 +2.17	2.92	-0.53
2AT98-2-1	104 -2.66	117 +2.52	125 +1.17	112 -3.21	110 -5.98	112 +2.55	107 -0.25	117 +0.38	115 +4.02	112 +1.43	3.09	-3.99
3AT10	110 +0.73	117 +0.31	126 -0.94	115 -2.52	117 -0.59	114 +1.54	110 +0.24	118 -0.23	117 +3.51	111 -2.08	1.74	-1.68
Standard deviation of SCA effects	2.68	1.69	4.18	1.83	3.23	3.20	2.20	2.61	3.55	2.92		
GCA effects	-6.74	+1.58	+11.03	+2.41	+2.28	-3.25	-5.85	+3.23	-2.42	-2.23		

S.E. GCA = 0.68 cm
S.E. SCA = 2.03 cm

Table 10. GCA and SCA effects of the 100 crosses relative to the number of two-eared plants per plot. The upper number is the mean for the cross and the lower is the SCA effect.

	SCA effects											
Parents	3BS1	3BS2	3BS5	3BS6	3BS7	2BT40	3BT1	3BT2	3BT5	3BT8	Standard deviation of SCA effects	GCA effects
3AS2	7.5 +0.01	9.9 +0.20	7.7 -1.28	9.1 -0.88	9.4 +0.90	12.4 +2.36	7.8 -1.23	13.1 -0.17	5.3 -0.66	11.4 +0.75	1.12	+3.76
3AS3	2.4 -0.36	8.2 +3.17	3.9 -0.30	5.4 +0.19	3.5 -0.25	3.6 -1.74	5.2 +0.90	9.8 +1.31	0.2 -1.03	4.1 -1.88	1.51	-0.99
3AS6	2.3 -0.67	3.5 -1.69	6.4 +2.05	5.3 -0.06	3.5 -0.44	3.2 -2.28	5.6 +1.04	10.6 +1.88	0.9 -0.51	6.8 +0.69	1.42	-0.79
3AS12	3.8 0.00	5.3 -0.75	7.6 +2.33	7.4 +1.18	5.6 +0.78	3.3 -3.05	6.2 +0.81	9.5 -0.12	0.9 -1.34	7.2 +0.19	1.48	+0.10
3AS15	4.0 +2.05	3.9 -0.31	2.0 -1.40	3.4 -0.96	3.1 +0.17	3.4 -1.07	5.1 +1.58	6.3 -1.40	0.9 +0.48	6.0 +0.85	1.24	-1.78
3AT3	6.1 +1.34	7.6 +0.59	5.0 -1.17	6.9 -0.23	6.1 +0.40	7.4 +0.10	5.7 -0.64	11.7 +1.21	1.7 -1.51	7.8 -0.08	0.94	+0.99
3AT6	0.7 +1.18	0.7 -0.10	1.1 +0.19	2.2 +0.24	1.1 +0.59	1.5 -0.53	1.3 +0.23	2.4 -2.87	0.0 +2.08	2.6 -0.11	1.32	-4.26
3AT15	3.4 -1.49	7.9 +0.81	5.2 -1.10	9.9 +2.55	7.1 +1.18	8.3 +0.89	4.9 -1.52	11.1 +0.42	1.8 -1.50	7.8 -0.24	1.40	+1.15
2AT98-2-1	4.3 -2.40	7.9 -1.08	9.9 +1.72	8.0 -1.18	6.3 -1.39	12.0 +2.71	7.1 -1.20	12.7 +0.21	6.8 +1.60	10.9 +1.01	1.69	+3.00
3AT10	2.9 +0.34	4.8 +0.06	2.9 -1.04	4.2 -0.83	1.6 -1.93	7.7 +2.62	4.2 +0.04	7.8 -0.48	3.4 +2.39	4.6 -1.18	1.49	-1.19
Standard deviation of SCA effects	1.34	1.37	1.49	1.14	1.01	2.10	1.09	1.39	1.53	0.93		
GCA effects	-1.87	+0.38	-0.43	+0.58	-0.87	+0.69	-0.29	+3.91	-3.42	+1.33		

S.E. GCA = 0.74
S.E. SCA = 2.20

Table 11. GCA and SCA effects of the 100 crosses relative to the percentage of erect plants. The upper number is the mean for the cross and the lower is the SCA effect.

	SCA effects											
Parents	3BS1	3BS2	3BS5	3BS6	3BS7	2BT40	3BT1	3BT2	3BT5	3BT8	Standard deviation of SCA effects	GCA effects (%)
3AS2	95 +5.06	91 -0.71	91 +3.32	74 +3.10	59 -3.83	92 -1.67	93 +9.90	86 -2.40	96 -4.54	64 -8.25	5.34	+4.52
3AS3	91 +1.06	91 -1.01	92 +4.52	75 +4.60	74 +10.17	82 -11.77	75 -8.90	85 -3.60	99 -1.64	79 +6.55	6.86	+4.92
3AS6	90 +2.52	88 -0.65	85 +0.48	65 -2.54	59 -0.97	94 +3.19	78 -2.34	83 -3.04	99 +0.92	72 +2.41	2.26	+1.86
3AS12	66 -11.27	79 -0.04	75 -0.11	61 +2.67	46 -4.66	88 +7.10	82 +10.97	70 -5.73	96 +7.73	53 -6.68	7.18	-7.95
3AS15	81 +1.87	80 -0.30	76 -0.27	58 -0.99	52 +0.28	84 +1.54	69 -3.49	73 -4.49	95 +6.07	61 -0.24	2.91	-6.49
3AT3	78 -3.87	86 +2.56	78 -0.71	62 -0.73	58 +3.34	92 +6.80	66 -8.63	86 +5.57	93 +0.93	59 -4.78	4.82	-3.55
3AT6	73 -5.43	75 -6.00	79 +2.23	55 -4.69	53 +0.88	85 +2.84	69 -2.89	85 +7.31	93 +4.17	62 +1.56	4.51	-6.59
3AT15	90 +4.35	88 +0.58	72 -10.89	71 +4.89	55 -3.34	91 +1.52	78 -1.21	90 +5.99	94 -1.85	68 -0.06	4.90	+0.23
2AT98-2-1	96 +4.90	97 +4.23	90 +1.26	72 +0.44	63 -1.89	90 -4.93	88 +3.24	90 +0.24	94 -7.80	74 +0.29	3.99	+5.98
3AT10	93 +0.79	96 +1.32	91 +0.65	66 -6.77	66 0.00	92 -4.64	89 +3.33	91 +0.13	99 -4.01	84 +9.18	4.49	+7.09
Standard deviation of SCA effects	5.29	2.68	4.19	3.91	4.31	5.84	6.84	4.73	4.94	5.49		
GCA effects	+5.75	+7.72	+3.49	-13.59	-20.96	+9.68	-0.89	+4.61	+16.35	-12.14		

S.E. GCA = 4.38 (%)
S.E. SCA = 13.15 (%)

3AS3, 2AT98-2-1, and 3AT10 were good combiners. In the B Group, 3BS1 and 3BS2 were good combiners with the S_2 progeny method and 2BT40 and 3BT5 were good combiners with the testcross method. This indicates that there was a similar number of lines with both the S_2 progeny method and the testcross method that were good for GCA. The ranges in GCA effects were -7.95 to +7.09 ± 4.38% and -20.96 to +16.35 ±4.38% for Parental Groups A and B, respectively.

Husk score is like ear height in that negative GCA effects are more desirable than positive GCA effects, because low scores which reflect good husk cover rating are desired for most maize breeding programs. In the A Group, with the S_2 progeny method two lines (3AS2 and 3AS12) were good combiners, while with the testcross method three lines (3AT6, 2AT98-2-1, and 3AT10) had good combining ability for husk cover (Table 12). The rest of the A Parents were relatively poor in GCA for husk score. The range in GCA effects was from -2.18 to +1.37 ±0.34. In the B Group, only 3BS6 with the S_2 progeny method was a good combiner, while with the testcross method 2BT40 and 3BT2 were good combiners for husk score. The range in GCA effects for the B Group was from -1.11 to +1.16 ±0.34.

Specific combining ability effects and their standard deviations (SD) for all traits are given in Tables 8-12. The ranges in SCA effects for grain yield, ear height, two-eared plants, erect plants, and husk cover were -0.864 to +0.816 ±0.78 Mg/plot, -6.50 to +6.72 ±2.03 cm, -3.05 to +3.17 ±2.20, -11.77

Table 12. GCA and SCA effects of the 100 crosses relative to the mean husk score. The upper number is the mean for the cross and the lower is the SCA effect.

	SCA effects										Standard deviation of SCA effects	GCA effects
Parents	3BS1	3BS2	3BS5	3BS6	3BS7	2BT40	3BT1	3BT2	3BT5	3BT8		
3AS2	5.6 −0.36	6.6 −0.32	5.8 +0.01	5.4 +0.07	5.2 −0.45	5.4 +0.39	5.7 0.00	5.1 +0.44	6.2 +0.34	6.4 −0.13	0.32	−0.24
3AS3	7.6 +0.28	7.5 −0.74	7.1 −0.02	6.7 −0.02	8.1 +1.08	6.3 −0.08	6.7 −0.30	6.2 +0.24	7.2 +0.04	7.4 −0.49	0.49	+1.12
3AS6	8.0 +0.48	8.7 +0.23	6.7 −0.70	6.8 −0.10	7.1 −0.22	7.4 +0.74	6.9 −0.32	6.2 0.00	7.8 +0.40	7.7 −0.51	0.46	+1.37
3AS12	5.6 −0.04	6.2 −0.40	5.6 +0.05	4.8 −0.28	5.8 +0.69	5.3 +0.54	4.2 −1.23	3.8 −0.52	6.6 +0.10	6.8 +0.47	0.67	−0.50
3AS15	5.8 −1.00	8.3 +0.53	6.3 −0.30	5.7 −0.53	5.5 −1.04	7.2 +1.31	6.7 +0.20	6.4 +0.96	6.9 +0.28	7.1 −0.38	0.79	+0.63
3AT3	6.6 +0.08	7.5 +0.01	6.2 −0.16	6.4 +0.51	6.9 +0.66	4.4 −1.27	7.4 +1.12	4.4 −1.53	6.9 +0.46	6.6 −0.62	0.85	+0.37
3AT6	5.9 +0.16	6.9 +0.19	6.7 +1.09	5.3 +0.20	6.2 +0.74	4.7 −0.14	5.7 +0.25	3.4 −0.98	3.6 −2.02	6.9 +0.50	0.90	−0.43
3AT15	6.2 −0.06	6.6 −0.68	6.3 +0.16	5.6 −0.12	5.7 −0.35	4.8 −0.63	6.7 +0.64	5.5 +0.52	6.8 +0.60	6.8 −0.09	0.48	+0.12
2AT98-2-1	4.1 +0.13	6.5 +1.56	3.6 −0.26	3.6 +0.18	3.0 −0.73	2.3 −0.83	3.0 −0.72	3.1 +0.44	3.3 −0.54	5.4 +0.76	0.77	−2.18
3AT10	6.2 +0.31	6.5 −0.37	5.9 +0.13	5.4 +0.08	5.6 −0.10	5.0 −0.04	6.0 +0.35	4.3 −0.33	5.3 −0.53	7.1 +0.50	0.34	−0.25
Standard deviation of SCA effects	0.42	0.68	0.46	0.28	0.72	0.78	0.68	0.76	0.86	0.51		
GCA effects	+0.19	+1.16	+0.04	−0.41	−0.06	−0.68	−0.07	−1.11	+0.09	+0.84		

S.E. GCA = 0.34
S.E. SCA = 1.03

to +10.17 ±13.15%, and -2.02 to +1.56 ±1.03, respectively. On the basis of standard deviations of SCA effects for the 25 crosses obtained by crossing the 3AS with the 3BS lines versus the 25 3AT by 3BT crosses, no significant difference was found between the S_2 progeny method and the testcross method. Thus, breeding method did not appear to influence SCA effects for any of the traits studied.

Correlation coefficients (r values) were calculated in order to compare GCA effects for grain yield with GCA for other traits (n = 20). There was no significant association between GCA effects for grain yield and ear height (r = 0.07) or between grain yield and erect plants (r = 0.10). For yield and two-eared plants, however, there was a significant correlation (r = 0.68). These results indicate that two-eared plants tended to be higher yielding than one-eared plants.

The results reported in this experiment have shown that the testcross method gave significantly better progress for combining ability in all traits than the S_2 progeny method. Nevertheless, a few lines from the S_2 progeny method had GCA as good as the best lines from the inbred tester method.

Similar results reported by Horner et al. (1973) showed that use of the inbred line F6 as the tester resulted in about twice as much improvement in GCA during five cycles of selection as use of the parental population as the tester or the S_2 progeny method. Baniya (1982), using a different base population, reported after two cycles of selection that both methods were effective in improving combining ability; the inbred tester method was significantly superior to the S_2 progeny method in Population A, based on crosses with both the inbred and population testers. Jensen et al. (1983) found with elite materials that evaluation of S_2 lines by the testcross method increased hybrid yields by 7%, compared with only 1% for S_2 per se evaluation. They concluded that the exploitable genetic variation in their elite germplasm was largely non-additive. Horner (1985) obtained no significant difference between methods for combining ability improvement, however, in a separate study of the same material used here. His study also showed that significant progress had been made with both methods. It was possible in the experiment reported on here to make a more precise comparison of the third-cycle populations than was done in the study reported on by Horner (1985). The factorial mating design produced a larger number of crosses for testing; populations from earlier cycles were not included; and more replications were used. The inbred tester method resulted in a 1% grain yield advantage (non-significant) over the S_2 progeny method after three cycles in the earlier experiment; in this experiment the inbred tester method had a significant 3% yield advantage for all crosses and a 7% advantage when only the 50 within-method crosses (A x B) are considered.

Experiment II: Determination of Inbreeding Depression

There were statistically significant differences among generations for all traits except erect plants and husk score

(Table 13). For yield, ear weight, and ear height there were significant decreases as the inbreeding coefficient increased. Ears per plant did not change from the Syn-1 to the S_1 generation, but decreased significantly from S_1 to S_2 (Table 17). The generations by environments interaction mean square was also significant at the 0.01 level for grain yield and ear weight, but was not significant for the other traits.

The S_2 progeny method was significantly better than the testcross method ($P<0.01$) for grain yield at the S_1 and S_2 levels of inbreeding, whereas in the Syn-1 generation there was no significant difference between the two methods (Tables 14 and 15). Population B was higher yielding than Population A in the Syn-1, but the reverse occurred at the S_2 level. This indicates that less inbreeding depression occured in Population A than in Population B (Table 15). The different response of population resulted in a significant ($P<0.01$) method by populations interaction for the Syn-1.

Grain yields of the four selected third-cycle populations at three levels of inbreeding (Syn-1, S_1, and S_2) show that the S_2 progeny method resulted in significantly less inbreeding depression than the testcross method (Table 15). Similar results have been reported by Horner et al. (1969) for three cycles and by Horner et al. (1973) for five cycles. A multiple linear regression analysis (Fig. 1) shows a close fit to linearity ($R^2 = 0.99$) for the average of both populations. Predicted grain yields of homozygous lines from the third-cycle

Table 13. Mean squares from the analyses of variance for seven agronomic traits for comparison of generations (Syn-1, S_1, and S_2).

Source of variation	df	Mean square					
		Grain yield	Ear weight	Ear height	Ears/ plant	Erect plant	Husk$^+$ score
		Mg/ha	g	cm	no.	%	
Environments (E)	3	2.35**	60460.26**	2.20**	0.07	0.42**	4.98**
Reps/E	28	0.56	398.59	0.13	0.03	0.01	0.46
Generations (G)	2	188.08**	100002.91**	6.55**	0.18**	0.01	0.28
E X G	6	1.63**	1049.14**	0.08	0.06	0.00	0.14
Error	56	0.30	207.29	0.04	0.03	0.003	0.57
Total	95						

*, ** significant at the 0.05 and 0.01 probability levels, respectively.
+ scores were on a 1 (good) to 9 (poor) scale.

Table 14. Mean squares from the analyses of variance for grain yields of Syn-1, S_1, and S_2 bulks from the third-cycle populations developed by the S_2 progeny and testcross methods.

Source of variation	df	Generations		
		Syn-1	S_1	S_2
Environments (E)	3	5.99**	1.82**	2.97**
Reps/E	28	0.84	0.73	0.69
Composites (C)	3	2.00**	1.55**	4.34**
Methods (M)	1	0.02	4.34**	11.38**
Populations (P)	1	3.57**	0.30	1.42*
M X P	1	2.49**	0.01	0.29
E x C	9	1.24**	0.23	0.23
E X M	3	3.28**	0.34	0.12
E X P	3	1.89**	0.25	0.43
E X (M X P)	3	0.88	0.32	0.14
Error	84	0.28	0.34	0.26
Total	127			

*, ** significant at the 0.05 and 0.01 probability levels, respectively.

Table 15. Grain yields of Syn-1, S_1, and S_2 bulks from the third-cycle populations developed by the S_2 progeny and testcross methods. Average for two locations (1985-1986).

Method and population	Generations			Predicted+
	Syn-1	S_1	S_2	$S\infty$
	Mg/ha			
S_2 progeny method				
A (C3)	6.43	4.56	3.52	2.59
B (C3)	6.48	4.44	3.22	2.20
Mean	6.45	4.50	3.37	2.40
Testcross method				
A (C3)	6.17	4.17	2.83	1.84
B (C3)	6.78	4.09	2.72	1.37
Mean	6.47	4.13	2.77	1.60
L.S.D. Means (0.05)	0.26	0.29	0.25	

+ Yield of 100% homozygous lines predicted by linear regression.

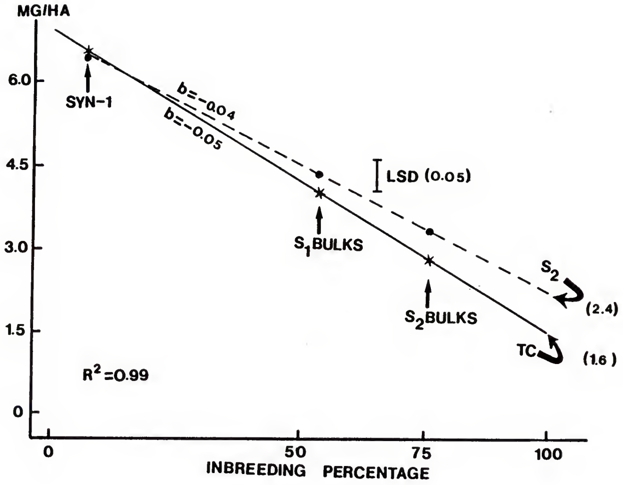

Figure 1. Inbreeding depression in cycle 3 populations developed by S_2 progeny (S_2) and testcross (TC) methods. Mean of two populations and two years for each method. Values at right are predicted yield of homozygous lines for the two methods.

populations were 2.4 and 1.6 Mg/ha for the S_2 progeny and testcross methods, respectively (Fig. 1). Thus, for grain yield of inbred generations, the S_2 progeny method was markedly superior to the testcross method in this experiment. This was expected because the S_2 progeny method places more emphasis on contributions of homozygous loci than heterozygous loci, while the reverse is true for the testcross method.

A summary of the analysis of variance and mean performance for characteristics other than yield is given in Tables 16 and 17. In Population A the S_2 progeny method resulted in significantly ($P<0.05$) higher ear weights at the first-generation synthetic and at the S_2 levels, but methods were not significantly different at the S_1 level of inbreeding. For ear weight in Population B, however, the S_2 progeny method was superior to the testcross method at all three levels of inbreeding. This resulted in a significant method by population interaction for the S_1 generation. Ears were significantly higher (undesirable) for the S_2 method at all three levels of inbreeding, and there was a significant ($P<0.01$) environment by population interaction for this trait. Number of ears per 100 plants was significantly different at the 0.05 level in Population B for Syn-1 and S_1. No significant difference was found for ear number in Population A at the same levels of inbreeding. At the S_2 level no significant difference was found in either population. For percentage of erect plants at harvest, significant differences among methods and populations

Table 16. Mean squares from the analyses of variance for agronomic traits for comparison of S_2 progeny and testcross methods of Syn-1, S_1, and S_2 generations (separate analyses).

Source of variation	df	Mean square					
		Ear weight			Ear height		
		Syn-1	S_1	S_2	Syn-1	S_1	S_2
Environ. (E)	3	62810.09**	34238.97**	26552.45**	1.38**	2.19**	1.19**
Reps/E	28	487.96	478.68	364.08	0.12	0.12	0.15
Composites (C)	3	1867.67**	1211.76**	2189.45**	0.20**	0.22*	0.42**
Methods (M)	1	4863.44**	2538.28**	6300.03**	0.54**	0.54**	1.26**
Populations (P)	1	182.88	84.50	205.03	0.03	0.11	0.00
M X P	1	556.94	1012.50**	63.28	0.02	0.01	0.00
E X C	9	263.94	55.34	235.39	0.07	0.02	0.03
E X M	3	71.20	47.05	163.03	0.04	0.02	0.05
E X P	3	62.91	95.23	306.53	0.07	0.01	0.03
E X (M X P)	3	657.76*	23.73	236.61	0.10	0.04	0.01
Error	84	240.05	134.96	170.48	0.04	0.07	0.04
Total	127						

Table 16--continued.

Source of variation	df	Mean square								
		Ears/plant			Erect plants			Husk score		
		Syn-1	S_1	S_2	Syn-1	S_1	S_2	Syn-1	S_1	S_2
Environments (E)	3	0.15*	0.11*	0.21**	0.28**	0.28**	0.27**	5.47**	2.77*	2.40**
Reps/E	28	0.04	0.04	0.07	0.01	0.02	0.01	0.93	1.58	0.67
Composites (C)	3	0.30**	0.18**	0.04	0.04**	0.00	0.00	3.94**	2.77*	3.46**
Methods (M)	1	0.54**	0.15*	0.02	0.04**	0.01	0.00	6.57**	8.00**	5.28**
Pop. (P)	1	0.05	0.01	0.08	0.07**	0.00	0.00	0.38	0.28	2.53*
M X P	1	0.29**	0.38**	0.02	0.00	0.00	0.00	4.88**	0.03	1.12
E X C	9	0.06**	0.02	0.03	0.02	0.00	0.01	0.77	0.88	1.45
E X M	3	0.02	0.05	0.03	0.01	0.00	0.01	0.63	1.27	0.47
E X P	3	0.10**	0.00	0.00	0.05**	0.01	0.01	0.32	0.10	3.68**
E X (M X P)	3	0.06*	0.00	0.06	0.01	0.00	1.00	1.03	1.26	0.52
Error	84	0.02	0.03	0.04	0.005	0.01	0.01	0.65	0.82	0.50
Total	127									

*, ** significant at the 0.05 and 0.01 probability levels, respectively.

Table 17. Mean performance for several traits of Syn-1, S_1, and S_2 bulks from the cycle 3 populations developed by the S_2 progeny and testcross methods. Average for two locations (1985-1986).

Population and method	Generation								
	Syn-1	S_1	S_2	Syn-1	S_1	S_2	Syn-1	S_1	S_2
	Ear weight g			Ear height cm			Ears/100 plants		
Pop. A									
S_2	169[+]	113	94	101	89	83	146	156	145
TC	161	109	79	96	86	77	150	152	145
Pop. B									
S_2	176	120	96	101	91	83	141	144	137
TC	160	105	83	98	87	77	164	161	142
L.S.D. (0.05)	8	6	6	3	4	3	7	9	ns

Table 17--continued.

Population and method	Generation					
	Syn-1	S_1	S_2	Syn-1	S_1	S_2
	Erect plants %			Husk score[++]		
Pop. A						
S_2	95	91	90	5.6	5.8	5.4
TC	92	89	89	5.6	5.2	5.2
Pop. B						
S_2	91	89	89	5.9	5.6	5.8
TC	87	88	89	5.1	5.2	5.2
L.S.D. (0.05)	3.5	ns	ns	0.4	0.4	0.3

+ Each mean represents 32 observations.
++ scores were on a 1 (good) to 9 (poor) scale.
ns nonsignificant.

were detected in the Syn-1, but neither effect was significant in the S_1 and S_2 bulks. There was also a significant ($P<0.01$) environment by population interaction for erect plants in the Syn-1. Husk ratings were significantly higher (undesirable) for the S_2 method at all three levels of inbreeding. Interaction of environments by populations was significant ($P<0.01$) only for the S_2 level.

The significant environment by population interaction for husk score, percentage of erect plants, and ears per plant may have been caused by fertility levels and different rainfall patterns at these locations during the two years, which could have had differential effects on the Cycle 3 populations of different maturities. Such trend was also reported by Zambezi et al. (1986) for hybrids of different maturity.

Experiment III: Yield of Selected C4 Lines from Each Population and Method

Variation among the four composites was significant at the 0.01 level for all traits studied except erect plants (Table 18). Interaction between composites and locations was significant at the 0.01 level only for grain yield. There were statistically significant differences between methods for all traits analyzed except erect plants (Table 18). Populations were also significantly different at the 0.01 level for grain yield and number of ears per plant and at 0.05 level for ear height and husk score. No significant

Table 18. Mean squares from the analyses of variance for several traits for comparison of S_2 progeny and testcross methods of fourth-cycle populations.

Source of variation	df	Trait					
		Grain yield	Ear weight	Ear height	Ears/ plant	Erect plant	Husk$^+$ score
		Mg/ha	g	cm	no.	%	
Locations (L)	1	4.02**	1757.81*	0.001	0.36*	0.10**	3.61
Reps/L	18	0.37	303.70	0.07	0.05	0.01	1.39
Composites (C)	3	3.60**	2497.75**	0.50**	0.17**	0.02	10.75**
Methods (M)	1	6.11**	7353.61**	0.70**	0.22**	0.02	15.31**
Populations (P)	1	1.67**	99.02	0.33*	0.25**	0.00	9.11*
M X P	1	3.03**	40.61	0.46*	0.04	0.04	7.82*
L X C	3	0.82**	68.21	0.06	0.02	0.03	0.81
L X M	1	0.00	0.61	0.01	0.00	0.00	0.01
L X P	1	2.46**	183.01	0.10	0.06	0.04	0.11
L X (M X P)	1	0.00	21.01	0.08	0.00	0.04	2.33
Error	54	0.13	121.44	0.08	0.02	0.01	1.48
Total	79						

*, ** significant at the 0.05 and the 0.01 probability levels, respectively.
+ scores were on a 1 (good) to 9 (poor) scale.

difference between populations was found for ear weight or erect plants at harvest. In Population A, the two methods were significantly different for yield, the S_2 progeny method being significantly superior at the 0.05 level; whereas in Population B there was no significant difference for yield between the two methods (Tables 18 and 19). This resulted in a significant method by population interaction.

The S_2 progeny method resulted in significantly heavier ears in both populations than the testcross method (Table 19). The S_2 progeny method resulted in significantly higher ears in Population A; whereas in Population B there was no significant difference between the two methods. The number of ears per 100 plants was higher in Population A than in Population B. However, in population A no significant difference between the two methods was observed. In Population B, the testcross method resulted in significantly more ears per 100 plants at the 0.05 level than the S_2 progeny method. The testcross method resulted in significantly ($P<0.05$) better husk score (low husk cover scores are more desirable than high scores) than the S_2 progeny method in Population B, but no significant difference was found in Population A. The larger ears with S_2 progeny method may have resulted in shorter husk and, therefore, higher husk scores.

In summary, these data (Table 19) show that there was a trend for higher grain yield (Population A), higher ear weight, taller (undesirable) ear height, same number of ears

Table 19. Mean performance for several traits of cycle-4 lines selected by the S_2 progeny and testcross methods. Average for two locations (1986).

	Trait					
	Grain yield	Ear weight	Ear height	Ears/ 100 plants	Erect plant	Husk score
	Mg/ha	g	cm	no.	%	
Pop. A						
S_2	3.85[+]	116	83.4	159	92	6.0
TC	2.92	95	73.2	159	85	5.8
Pop. B						
S_2	3.00	117	82.5	140	91	6.0
TC	3.18	99	81.6	158	89	4.5
L.S.D. (0.05)	0.23	7	3.8	11	ns	0.8

+ Each mean represents 20 observations.
ns nonsignificant

per 100 plants in Population A but fewer in Population B, more erect plants at harvest, and higher (poorer) husk score with the S_2 progeny method than with the testcross method.

The two experiments (II and III) on effect of methods on vigor of inbred lines derived from third and fourth cycle populations and on inbreeding depression have produced similar results. The second experiment showed (Table 14) that the S_2 progeny method was superior to the testcross method for grain yield of third-cycle populations in the S_1 and S_2 generations. The third experiment showed (Table 19) that the S_2 progeny method was superior to the testcross method for grain yield in Population A; however, in Population B no significant difference was detected. A possible explanation for the lack of difference between methods in Population B is that more intensive selection for agronomic type and vigor was necessary in this Population than in Population A, possibly because it contained more tall plants of poor agronomic type. This visual selection may have resulted in equal progress for both methods in Population B. The overall yield performance (average of both populations and both experiments) was better with the S_2 progeny method than with the testcross method.

Experiment IV: Correlation of Inbred Lines (S_2 Parents) and Testcross Performance.

Simple correlation coefficients for five traits observed in the 1984 screening tests are presented in Table 20.

Table 20. Simple correlation coefficients between S_2 lines and testcross performance for five traits in 1984.

Trait	Population A	Population B
Stalk quality	0.36 **	0.51 **
Ear height	0.57 **	0.42 **
Husk score	0.58 **	0.62 **
Ear quality	0.20 **	0.17 **
Ears per plant	0.30 **	0.10 ns

** Significantly larger than zero at the 0.01 level (276 df).
ns nonsignificant

Inbred line and testcross performances were positively correlated for all traits studied, except ears per plant in Population B. Even though the two methods were positively correlated, however, the R^2 values were small. The highest R^2 was equal to 0.38 for the correlation of husk score in S_2 lines and testcrosses in Population B. The simple correlation between S_2 and testcross ear height was significantly larger for Population A ($r = 0.57$) than Population B ($r = 0.42$). Conversely, for stalk quality in Population B the correlation between S_2 lines and their testcrosses ($r = 0.51$) was significantly greater than that of the Population A ($r = 0.36$). Correlations between S_2 and testcross husk score entry means were the largest of any calculated ($r = 0.58$ and $r = 0.62$) for Populations A and B, respectively. However, for ear quality and particularly for ears per plant, correlations of performance between S_2 lines and testcrosses seem of little value. These results, which are similar to those reported by Clucas (1985), indicate that visual selection among lines in one environment may be effective for the elimination of undesirable traits in hybrids, especially for stalk strength, ear height and husk score. However, these results are in disagreement with those of e Gama and Hallauer (1977), who found very low correlations for plant and ear traits between S_7 lines from BSSS and their single cross hybrids. Maybe such highly homozygous lines (S_7) are more subject to genotype by environment interaction than S_1 or S_2 lines.

CONCLUSIONS

The two breeding methods apparently emphasize different types of gene action, as would be expected from genetic theory. The S_2 progeny method places more emphasis on the contribution of alleles in the homozygous state, which resulted in appreciably higher yielding inbred lines in the third cycle than were obtained with the inbred tester method. The inbred tester method, on the other hand, emphasizes the contribution of heterozygous loci which resulted in slightly higher combining ability than was obtained with the S_2 progeny method. These results suggest the possibility of overdominant gene action at some loci. More cycles of selection are needed to determine the long-term effects of these contrasting breeding methods.

LITERATURE CITED

Baniya, B. K. 1982. Evaluation of two methods of maize (Zea mays L.) improvement after two cycles of selection. Master's thesis. Univ. of Fla., Gainesville.

Beal, W. J. 1880. Indian corn. Rep., Mich. Board Agric. 19:279-289.

Brieger, F. G. 1950. The genetic basis of heterosis in maize. Genetics 35:420-445.

Burton, J. W., L. H. Penny, A. R. Hallauer, and S. A. Eberhart. 1971. Evaluation of synthetic populations developed from a maize variety (BSK) by two methods of recurrent selection. Crop Sci. 11:361-365.

Caranjal, V. R., S. M. Ali, A. F. Koble, E. H. Rinke, and J. C. Sentz. 1971. Comparison of S_1 with testcross evaluation for recurrent selection in maize. Crop Sci. 11:658-661.

Choo, T. M., and L. W. Kannenberg. 1979. Relative efficiencies of population improvement methods in corn: A simulation study. Crop Sci. 19:179-185.

Clucas, C. P. 1985. Effects of visual selection among and within lines of maize on S_2 line and testcross performance. Ph.D. dissertation. Iowa State Univ., Ames.

Comstock, R. E. 1964. Selection procedures in corn improvement. p. 87-94. In Proc. 19th Annual Hybrid Corn Ind.-Res. Conf., Chicago, IL. 8 Dec. 1964. American Seed Trade Association. Washington, DC.

Comstock, R. E. 1979. Inbred lines vs. the population as testers in reciprocal recurrent selection. Crop Sci. 19:881-886.

Comstock, R. E., and H. F. Robinson. 1952. Estimation of average dominance of genes. p. 494-516. In J. W. Gowen (ed.). Heterosis. Iowa State Univ. Press, Ames, Iowa.

Comstock, R. E., H. F. Robinson, and P. H. Harvey. 1949. A breeding procedure designed to make maximum use of both general and specific combining ability. Agron. J. 41:360-367.

Cress, C. E. 1966. A comparison of recurrent selection systems. Genetics 54:1371-1379.

Cress, C. E. 1967. Reciprocal recurrent selection and modifications in simulated populations. Crop Sci. 7:561-567.

Crow, J. F. 1948. Alternative hypothesis of hybrid vigor. Genetics 33:477-487.

Darrah, L. L., S. A. Eberhart, and L. H. Penny. 1972. A maize breeding methods study in Kenya. Crop Sci. 12:605-608.

Darrah, L. L., S. A. Eberhart, and L. H. Penny. 1978. Six years of maize selection in 'Kitale synthetic II', 'Ecuador 573', and 'Kitale composite A' using methods of the comprehensive breeding system. Euphytica 27:191-204.

da Silva, W. J., and J. H. Lonnquist. 1968. Genetic variances in populations developed from full-sib and S_1 testcross progeny selection in an open-pollinated variety of maize. Crop Sci. 8:201-204.

Davis, R. L. 1927. Report of the plant breeder. Puerto Rico Agric. Exp. Stn. Rep. p. 14-15.

Davis, R. L. 1934. Maize crossing values in second-generation lines. J. Agric. Res. 48:339-357.

Duclos, L. A., and P. L. Crane. 1968. Comparative performance of topcrosses and S_1 progeny for improving population of corn (Zea mays L.). Crop Sci. 8:191-194.

East, E. M. 1936. Heterosis. Genetics 21:375-397.

Eberhart, S. A., S. Debela, and A. R. Hallauer. 1973. reciprocal recurrent selection in the BSSS and BSCB1 maize populations and half-sib selection in BSSS. Crop Sci. 13:451-456.

Eberhart, S. A., R. H. Moll, H. F. Robinson, and C. C. Cockerman. 1966. Epistatic and other genetic variances in two varieties of maize. Crop Sci. 6:275-280.

e Gama, Elto E. G., and A. R. Hallauer. 1977. Relation between inbred and hybrid traits in maize. Crop Sci. 17:703-706.

Gardner, C. O. 1963. Estimates of genetic parameters in cross fertilizating plants and their importance in plant breeding. p. 225-248. In W. D. Hanson and H. F. Robinson (eds.). Statistical genetics and plant breeding. NAS-NRC Publ. 982. Washington, DC.

Gardner, C. O., P. H. Harvey, R. E. Comstock, and H. F. Robinson. 1953. Dominance of genes controlling quantitative characters in maize. Agron. J. 45:186-191.

Gardner, C. O., and J. H. Lonnquist. 1959. Linkage and the degree of dominance of genes controlling quantitative characters in maize. Agron. J. 51:524-528.

Genter, C. F. 1973. Comparison of S_1 and testcross evaluation after two cycles of recurrent selection in maize. Crop Sci. 13:524-527.

Genter, C. F., and M. W. Alexander. 1962. Comparative performance of S_1 progenies and testcrosses in corn. Crop Sci. 2:516-519.

Genter, C. F., and M. W. Alexander. 1966. Development and selection of productive S_1 inbred lines of corn (*Zea mays* L.). Crop Sci. 6:429-431.

Genter, C. F., and S. A. Eberhart. 1974. Performance of original and advanced maize populations and their diallel crosses. Crop Sci. 14:881-885.

Goulas, C. K., and J. H. Lonnquist. 1977. Comparison of combined half-sib and S_1 family selection with half-sib, S_1, and selection index procedures in maize. Crop Sci. 17:754-757.

Griffing, B. 1962. Prediction formulae for general combining ability selection methods utilizing one or two random-mating populations. Aust. J. of Biol. Sci. 15:650-665.

Hallauer, A. R. 1984. Reciprocal full-sib selection in maize. Crop Sci. 24:755-759.

Harris, R. E., C. O. Gardner, and W. A. Compton. 1972. Effect of mass selection and irradiation in corn measured by random S_1 lines and their testcrosses. Crop Sci. 12:594-598.

Hopkins, C. G. 1899. Improvement in the chemical composition of the corn kernel. Ill. Agric. Exp. Stn. Bull. 55:205-240.

Horner, E. S. 1963. A comparison of S_1 lines and S_1 plant evaluation for combining ability in corn (Zea mays L.). Crop Sci. 3:519-522.

Horner, E. S. 1968. Effect of a generation of inbreeding on genetic variation in corn (Zea mays L.) as related to recurrent selection procedures. Crop Sci. 8:32-35.

Horner, E. S. 1985. Effects of selection for S_2 progeny versus testcross performance in corn. p. 142-150. In Proc. 40th Ann. Corn and Sorghum Industry Res. Conf., Chicago, IL. 12 Dec. 1985. American Seed Trade Association. Washington, DC.

Horner, E. S., W. H. Chapman, M. C. Lutrick, and H. W. Lundy. 1969. Comparison of selection based on yield of topcross progenies and of S_2 progenies in maize (Zea mays L.). Crop Sci. 9:539-543.

Horner, E. S., H. W. Lundy, M. C. Lutrick, and W. H. Chapman. 1973. Comparison of three methods of recurrent selection in maize. Crop Sci. 13:485-489.

Horner, E. S., S. L. Robinson, and M. Ameha. 1977. S_2 line per se versus testcross yields in corn. p. 21-31. In Proc. 32nd Annual Corn and Sorghum Ind.-Res. Conf., Chicago, IL. 8 Dec. 1977. American Seed Trade Association. Washington, DC.

Hull, F. H. 1945. Recurrent selection for specific combining ability in corn. J. Amer. Soc. Agron. 37:134-145.

Jenkins, M. T. 1935. The effect of inbreeding and of selection within inbred lines of maize upon the hybrids made after successive generations of selfing. Iowa State Coll. J. Sci. 6:429-450.

Jenkins, M. T. 1940. The segregation of genes affecting yield of grain in maize. J. Amer. Soc. Agron. 32:55-63.

Jenkins, M. T., and A. M. Brunson. 1932. Methods of testing inbred lines of maize in cross-bred combinations. J. Amer. Soc. Agron. 24:523-530.

Jensen, S. D., W. E. Kuhn, and R. L. McConnell. 1983. Combining ability studies in elite U.S. maize germplasm. p. 87-96. In Proc. 38th Annual Corn and Sorghum Ind.- Res. Conf., Chicago, IL. 8 Dec. 1983. American Seed Trade Association. Washington, DC.

Jones, D. F. 1917. Dominance of linked factors as a means of accounting for heterosis. Genetics 2:466-477.

Jones, D. F. 1918. The effects of inbreeding and crossbreeding upon development. Conn. Agric. Exp. Stn. Bull. 207:5-100.

Koble, A. F., and E. H. Rinke. 1963. Comparative S_1 line and topcross performance in maize. p. 83. In Agron. Abstr. 55th Annual Meeting. Denver, CO. 17 Nov. 1963. American Society of Agronomy. Madison, WI.

Lindsey, M. F., J. H. Lonnquist, and C. O. Gardner. 1962. Estimates of genetic variance in open-pollinated varieties of Cornbelt corn. Crop Sci. 2:105-108.

Lonnquist, J. H. 1949. Development and performance of synthetic varieties of corn. Agron. J. 41:153-156.

Lonnquist, J. H. 1968. Further evidence on testcross versus line performance in maize. Crop Sci. 8:50-53.

Lonnquist, J. H., and M. G. Castro. 1967. Relation of intrapopulation genetic effects to performance of S_1 lines of maize. Crop Sci. 7:361-364.

Lonnquist, J. H., and C. O. Gardner. 1961. Heterosis in inter-varietal crosses in maize and its implication in breeding procedures. Crop Sci. 1:179-183.

Lonnquist, J. H., and M. F. Lindsey. 1964. Topcross versus S_1 line performance in corn (Zea mays L.). Crop Sci. 4:580-584.

Martin, J. M., and A. R. Hallauer. 1980. Seven cycles of reciprocal recurrent selection in BSSS and BSCB1 maize populations. Crop Sci. 20:599-603.

Matzinger, D. F., G. F. Sprague, and C. C. Cockerham. 1959. Diallel crosses of maize in experiments repeated over locations and years. Agron. J. 51:346-350.

Moll, R. H., C. C. Cockerham, C. W. Stuber, and W. P. Williams. 1978. Selection responses, genetic-environmental interactions and heterosis with recurrent selection for yield in maize. Crop Sci. 18:641-645.

Moll, R. H., and W. D. Hanson. 1984. Comparisons of effects of intrapopulation vs. interpopulation selection in maize. Crop Sci. 24:1047-1052.

Moll, R. H., M. F. Lindsey, and H. F. Robinson. 1964. Estimates of genetic variances and level of dominance in maize. Genetics 49:411-423.

Moll, R. H., and H. F. Robinson. 1967. Quantitative genetic investigations of yield in maize. Der Zuchter 37:192-199.

Moll, R. H., and O. S. Smith. 1981. Genetic variances and selection responses in an advanced generation of a hybrid of widely divergent populations of maize. Crop Sci. 21:387-391.

Moll, R. H., and C. W. Stuber. 1971. Comparisons of response to alternative selection procedures indicated with two populations of maize (Zea mays L.). Crop Sci. 11:706-711.

Murkherjee, B. K., R. D. Singh, K. N., Agarwal, and V. P. Ahuja. 1980. Relative performance of maize populations synthesized from various types of progenies. Indian J. Agric. Sci. 50:462-465.

Penny, L. H., W. A. Russell, and G. F. Sprague. 1962. Types of gene action in yield heterosis in maize. Crop Sci. 2:341-344.

Robinson, H. F., R. E. Comstock, and P. H. Harvey. 1949. Estimates of heritability and the degree of dominance in corn. Agron. J. 41:353-359.

Robinson, H. F., R. E. Comstock, and P. H. Harvey. 1955. Genetic variances in open-pollinated varieties of corn. Genetics 40:45-60.

Robinson, S. L. 1976. Selection with an inbred tester versus S_2 line selection in maize. Master's thesis. Univ. of Fla., Gainesville.

Rojas, B. A., and G. F. Sprague. 1952. A comparison of variance components in corn yield trials: III. General and specific combining ability and their interaction with locations and years. Agron. J. 44:462-466.

Russell, W. A. 1971. Types of gene action at three gene loci in sub-lines of a maize inbred line. Can. J. Gen. Cytol. 13:322-334.

Russell, W. A., and S. A. Eberhart. 1975. Hybrid performance of selected maize lines from reciprocal recurrent and testcross selection programs. Crop Sci. 15:1-4.

Russell, W. A., S. A. Eberhart, and Urbano A. Vega O. 1973. Recurrent selection for specific combining ability for yield in two maize populations. Crop Sci. 13:257-261.

Shull, G. H. 1910. Hybridization methods in corn breeding. Amer. Breeders Assoc. 2:98-107.

Smith, O. S. 1979. Application of a modified diallel analysis to evaluate recurrent selection for grain yield in maize. Crop Sci. 19:819-822.

Smith, O. S. 1986. Covariance between line per se and testcross performance. Crop Sci. 26:540-543.

Sprague, G. F. 1939. An estimation of the number of topcrossed plants required for adequate representation of corn variety. J. Amer. Soc. Agron. 31:11-16.

Sprague, G. F. 1983. Heterosis in maize. Theory and practice. p. 47-70. In G. R. Frankel (ed.). Heterosis reappraisal of theory and practice. Monographs on Theoretical and applied Genetics. Springer-Verlag, Berlin.

Sprague, G. F., and S. A. Eberhart. 1977. Corn breeding. p. 305-362. In G. F. Sprague (ed.). Corn and corn improvement. Amer. Soc. Agron., Madison, Wisc.

Sprague, G. F., and P. A. Miller. 1950. A suggestion for evaluating current concepts of the genetic mechanism of heterosis in corn. Agron. J. 42:161-162.

Sprague, G. F., W. A. Russell, and L. H. Penny. 1959. Recurrent selection for specific combining ability and type of gene action involved in yield heterosis in corn. Agron. J. 51:392-394.

Sprague, G. F., and L. A. Tatum. 1942. General vs. specific combining ability in single crosses of corn. J. Amer. Soc. Agron. 34:923-932.

Stuber, C. W., and R. H. Moll. 1969. Epistasis in maize (*Zea mays* L.). F_1 hybrids and their S_1 progeny. *Crop Sci.* 9:124-127.

Tanner, A. H. 1984. Comparison of half-sib and S_1 recurrent selection in Krug yellow dent. Ph.D. dissertation. Iowa State Univ., Ames.

Thompson, D. L., W. D. Hanson, and A. W. Shaw. 1971. Ear height inheritance estimates and linkage bias among generation means of corn. Crop Sci. 11:328-331.

Torregroza, M., and D. D. Harpstead. 1965. Performance of S_1 lines of maize per se and testcross to related and unrelated varieties. p. 21. In Agron. Abstr. 57th Annual Meeting. Columbus, OH. 31 Oct. 1965. American Society of Agronomy. Madison, WI.

Walejko, R. N., and W. A. Russell. 1977. Evaluation of recurrent selection for specific combining ability in two open-pollinated maize cultivars. Crop Sci. 17:647-651.

West, D. R., W. A. Compton, and M. A. Thomas. 1980. A comparison of replicated S_1 per se vs. reciprocal full-sib index selection in corn. I. Indirect response to population densities. Crop Sci. 20:35-42.

Wright, A. J. 1980. The expected efficiencies of half-sib, testcross and S_1 progeny testing methods in single population improvement. Heredity 45:361-376.

Zambezi, B. T., E. S. Horner, and F. G. Martin. 1986. Inbred lines as testers for general combining ability in maize. Crop Sci. 26:908-910.

BIOGRAPHICAL SKETCH

Jorge Morera was born July 11, 1950, in Alajuela Province, Costa Rica. He completed high school at the Institute of Alajuela in 1970. He attended the University of Costa Rica in 1971 and received the degree of Ingeniero Agronomo in December 1976. In July 1976, he was appointed research-plant breeder by the Ministerio de Agricultura y Ganaderia (1976-1978). In February 1978, he was granted a scholarship by Centro Internacional de Agricultura Tropical (CIAT) for training in plant breeding. In October of 1979, he accepted a position as a researcher in the Centro Agronomico Tropical de Investigacion y ensenanza. In March 1980, he attended the University of Costa Rica (UCR-CATIE), and received the degree of Master of Science in September 1981. In August 1983, the German Academic Exchange Service granted a scholarship to initiate his studies at the University of Florida. In January 1984, he began his graduate study program at the University of Florida where he is presently a candidate for the Ph.D. degree in genetics and plant breeding. He expects to go back to Costa Rica in December 1986 and work as a plant breeder in the Genetic Resources Program.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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